REPRODUCTIVE BIOLOGY OF SELECTED AQUATIC PLANTS

Robert R. Haynes[1]

ABSTRACT

Aquatic weeds are species that inhabit bodies of water in such quantities that they either interfere with man's usage or become a health hazard by serving as a breeding area for insects, especially mosquitoes. These plants are most often introduced species. They increase in numbers mostly by vegetative reproduction, including stem or leaf fragmentation, budding, or turion formation. For dioecious species in which only one sex occurs in an area, vegetative means are the only methods of reproduction. Monoecious species or species with perfect flowers often produce viable seeds, which usually are not important for increasing the population size, as they are deposited in large mats and do not get enough light or other requirements for germination. Some species that reproduce sexually, such as Eichhornia azurea, *are self-sterile, but others, such as* Eichhornia crassipes *or* Ottelia alismoides, *are self-compatible.* Ottelia alismoides, *in fact, almost always is self-pollinated. Before the flowers open, the pollen tubes grow to the stigma from the anther. The flower eventually opens, but fertilization has already occurred. Pollination may be by insects (e.g.,* Hydrocharis morsus-ranae) *or by wind (*Potamogeton nodosus*); or it takes place at the surface of water by contact between stigma and anther (*Lagarosiphon*), by airborne pollen (*Hydrilla verticillata*), or by water-borne pollen (*Elodea canadensis*); or pollination may occur underwater (*Najas minor*).

Aquatic weeds are species that inhabit bodies of water in such quantities that they either interfere with man's usage or become a health hazard by serving as a breeding area for insects. Such species are often introduced. Cook (1987) discussed 12 species that he considered to be the most notorious aquatic invaders and pointed out that only one, *Trapa natans*, relies on sexual processes for its reproduction and spread. Of the remaining 11, he noted that only *Myriophyllum spicatum*, *Najas minor*, and *Pistia stratiotes* regularly develop seed in their native and adventive ranges. *Salvinia molesta* is a sterile hybrid, and the rest have well-developed self-incompatibility mechanisms.

An understanding of their reproductive biology, both sexually and vegetatively, is important in developing methods of control for aggressive species. Aquatic flowering plants have pollinating systems ranging from those independent of the aquatic environment, such as wind and animal, to varying degrees of adaptation to the aquatic environment, beginning with pollination at the surface of the water, to underwater pollination with the pollen adhering to the surface of air bubbles, to a totally aquatic system in which pollen sinks in the water. The following selected list of aquatic weeds begins with the least adapted to the aquatic environment and terminates with the most adapted.

INSECT POLLINATED

Eichhornia crassipes (C. Mart.) Solms-Laub. (Pontederiaceae). Water-hyacinth.

Water-hyacinth is a free-floating annual or perennial with rosettes, well-developed stolons, and swollen to bulbous petiole bases. It is native to tropical South America but has been introduced ornamentally into warmer parts of all continents for its showy blue flowers (Barrett, 1982; Cook, 1987). *Eichhornia crassipes* spreads vegetatively by daughter rosettes that form rapidly on brittle stolons and separate from floating mats quite easily (Barrett, 1979).

Water-hyacinth is tristylous and self-compatible (Barrett, 1979). Barrett (1980a) studied fertility of nine clones of *Eichhornia crassipes* from different regions of the world. Eight of the nine populations flowered regularly during the study period and the ninth flowered frequently following the study period. Artificial crosses, both selfed and outcrossed, were made with each clone that flowered during the study period, totaling 2,546 crosses. Of these, 94.7% produced capsules, with an average of 143.3 seeds per capsule. All populations exhibited a high degree of self-compatibility, although degree of seed production varied among clones. Percentage of capsule set was significantly higher

[1] *Department of Biology, The University of Alabama, Tuscaloosa, Alabama 35487-1927, U.S.A.*

among all of the out-crossed than among all of the selfed plants.

A similar amount of seed production has been found in natural populations (Barrett, 1980b). He studied open-pollinated and artificially pollinated plants from 19 populations, with capsule production ranging from 72.3% to 100% per month for artificial pollinations, whereas it ranged from 8.1 to 68.7% for open-pollinated plants. Seeds per capsule were considerably fewer in open-pollinated ones, ranging from a mean of 3.1 to 40.8 per capsule, compared with artificially pollinated ones of 74.1 to 188.7 per capsule.

According to Barrett (1980b), *Eichhornia crassipes* can begin flowering 10–15 weeks after germination, soon for a perennial. One inflorescence with 20 flowers has the potential of producing 3,000 seeds, and up to four inflorescences can be produced by a single rosette during a 21-day period. Since flowering in subtropical to subtemperate regions may occur over five to nine months, the species can produce astronomical numbers of seeds. Regardless, most individuals in natural populations are probably produced vegetatively.

Seedlings were observed in only three of the 19 populations studied by Barrett (1980b). Apparently, seeds produced in dense floating mats of water-hyacinth either sink to the bottom or accumulate in the mat. Shading from the mats or low light levels coupled with low temperatures in deep water prevent the seeds from germinating.

Eichhornia azurea (Sw.) Kunth (Pontederiaceae). Rooted water-hyacinth.

Rooted water-hyacinth is an attached perennial with distichous, linear submersed leaves and elliptic to obovate floating leaves. The inflorescence is a compact spike of blue flowers, each having erose perianth lobes and a bilobed yellow spot in the center of the upper lobe. Vegetative reproduction is by chance fragmentation of the robustly branched stems (Barrett, 1978). The species is native to the Neotropics (Horn, 1987) and has been introduced to various regions as an ornamental (Barrett, 1978).

Unlike *Eichhornia crassipes*, *E. azurea* is tristylous and partially self-sterile. Barrett (1978) artificially selfed long-styled forms with the low-level anthers. Only 12% fruit set occurred. In contrast, when mid-level anthers were utilized, 94% fruit set occurred. A semihomostylous race has been observed in Costa Rica. This one has one whorl of anthers about the same level as the stigma. High seed set occurs when pollen from this anther whorl is used for selfing.

Ottelia alismoides (L.) Persoon (Hydrocharitaceae). Duck-lettuce.

Duck-lettuce is an annual or perennial from attached basal rosettes, with long-petiolate orbicular to ovate leaves. The flowers are borne singularly in solitary spathes terminating long scapes. They are perfect or very rarely imperfect (Cook & Urmi-König, 1984b), fragrant, and have staminodia that are important in attracting insect visitors. Cook (1982) indicated that, although no field observations have been published, the species is almost certainly insect pollinated. He also indicated that it is highly self-compatible and occasionally cleistogamous.

The plants are weeds of rice fields in the southern United States (Dike, 1969), Italy, and Southeast Asia (Cook & Urmi-König, 1984b). Increase in population size is apparently by seed, since no specialized means of vegetative propagation occurs (Cook & Urmi-König, 1984b).

Egeria densa Planchon (Hydrocharitaceae). Brazilean-elodea.

Brazilean-elodea is a rooted perennial with cauline leaves that are mostly in whorls of four. The flowers are imperfect and solitary on axillary peduncles that project the flowers to or above the water surface. Staminate and carpellate flowers contain glistening green functional nectaries. The flowers are frequently visited by small Diptera (Cook & Urmi-König, 1984a), but there is no evidence yet as to whether these insects are important in pollen transfer, since seed-set is so rare in nature and in cultivation.

Egeria densa is native to southeastern Brazil, Uruguay, Argentina, and possibly Paraguay. The species has been introduced into North America, Europe, Asia, Africa, and Australia. Only in warm temperate and cool subtropical climatic regions has it developed into an aquatic weed. Outside its native range, only in Chile are carpellate flowers known (Cook & Urmi-König, 1984a). No specialized overwintering structures are produced. Stem fragments root readily and develop into new shoots, so rapidly that the species often quickly overgrows a lake. Spread of *Egeria densa* probably results from its popularity in aquaria.

Hydrocharis morsus-ranae L. (Hydrocharitaceae). European frogbit.

European frogbit is a free-floating, stoloniferous perennial with basal, petiolate leaves. The flowers are borne in spathes and terminate pedicels that project the flower well above the spathe. Cook (1982) indicated that the carpellate flowers possess staminodia modified into nectaries that secrete a nectar attractive to insects. The staminate flowers appear quite similar to the carpellate flowers but lack these nectaries. They apparently offer no reward, but rely on mimicking the nectar-bearing carpellate flowers for insect attraction.

Hydrocharis morsus-ranae first appeared in the Western Hemisphere in 1932 at the Ottawa Botanic Garden, where it was cultivated (Dore, 1968). It was first noticed as an escape in 1939 in the Rideau Canal, from which it spread into the Ottawa and St. Lawrence rivers (Dore, 1968) and into the United States in 1974 (Roberts et al., 1981). This spread may have been by seed and by hibernacula. Cook & Lüönd (1982b) indicated that the species can grow from one hibernaculum to cover an area of one meter in diameter in one season.

Pistia stratiotes L. (Araceae). Water-lettuce.

Pistia is a monotypic genus of rosulate-leaved, free-floating, stoloniferous plants occurring in subtropical and tropical Africa, Asia, and America. The leaves are densely short-pubescent and surround a single terminal spathe that has the spadix adnate to its median line. The plants are monoeceious, with staminate and carpellate flowers on one spadix.

Cook (1987) indicated that the species is probably mostly self-pollinated, possibly by insects. Wilson (1960) stated that in Florida the ovary of water-lettuce tends to enlarge and become inflated, but no seeds are produced. He suggested that this lack of seed-set is probably due to absence of pollinators. His suggestion would tend to support Cook's view of the species being insect pollinated.

Pistia is important because of its vegetative reproductive capabilities. New plants are produced at the ends of the stolons and are separated from the parent plant by fragmentation. The species can reproduce rapidly enough to clog waterways.

Wind Pollinated

Potamogeton nodosus Poiret (Potamogetonaceae). Floating pondweed.

Potamogeton nodosus is a perennial from elongate rhizomes with long-petiolate, lanceolate submersed and floating leaves with cuneate bases. The inflorescence is a compact spike held above the surface of the water (Haynes, 1978).

The species can cover huge areas of lakes in the southern United States. There are probably only one or a few clones, as *Potamogeton nodosus* increases in number mostly by rhizome growth. Pollination is predominantly anemophilous (Philbrick & Anderson, 1987). As such, the species is adapted for outcrossing.

Myriophyllum spicatum L. (Haloragaceae). Eurasian milfoil.

Eurasian milfoil is a submersed, rooted, stoloniferous perennial with whorled pinnately compound leaves and emergent imperfect flowers. The plants are monoecious and wind pollinated.

Myriophyllum spicatum is native to northern Eurasia (Cook, 1987) and has spread into the Western Hemisphere from Ontario and Quebec south to Florida and west to Wisconsin, Oklahoma, Texas, and Mexico, as well as to British Columbia, Washington, and California (Aiken, 1981). The species has often choked waterways (Coffey & McNabb, 1974), but in some places dramatic decline in the number of plants has occurred (Bayley et al., 1968; Elser, 1969) to the extent that the species no longer poses an environmental problem in these places.

Spread of Eurasian milfoil is mostly by vegetative fragment and seed (Cook, 1987).

Pollination at Surface of Water

Hydrilla verticillata (L. f.) Royle (Hydrocharitaceae). Hydrilla.

Hydrilla is a perennial, rooted plant with the lower nodes having opposite leaves and the upper nodes having whorls of three to eight leaves. The flowers are imperfect and are produced singly in the leaf axils. Carpellate flowers are sessile with an elongating hypanthium that projects the perianth and stigma to the water's surface. As the hypanthium elongates, the perianth is forced open by a gas bubble (Cook & Lüönd, 1982a). Upon reaching the water surface, the perianth lobes open further, forming a funnel that is underwater below and open to the air above. The stigmas are at the bottom of this funnel. The subsessile staminate flower buds are released from the spathe by pedicel abscission and float on the surface at about a 45° angle. An hour or more after the bud is released, the perianth segments retract slightly, with each anther adhering to the convex part of the perianth. Soon the perianth spreads horizontally on the water surface; shortly after this the stamens suddenly spring from a horizontal to a vertical position; the anthers burst and scatter pollen in the air. As the pollen falls, most grains land on the water and are lost for reproductive purposes, but some fall into the funnel-shaped perianth of a carpellate flower, contacting a stigma. This is apparently a risky method of pollination, but, according to Cook & Lüönd (1982a), seed production is adequate to maintain hydrilla populations in areas that dry out and where hibernacula are not produced, or at least have not been observed.

Most increase in plant density is by hibernacula, which occur in two forms. The first form is from erect stems and is olive green and ovoid-conical with spreading apices that give the structure the appearance of a sandbur. Hibernacula of the second type are brown, subterranean structures that appear as minute potatoes at the tips of long, stringy, white, leafless rhizomes. Cook & Lüönd (1982a) indicated that the first type has food reserves in leaves, whereas the second has food reserves in swollen stem tissue.

Lagarosiphon major (Ridley) Moss (Hydrocharitaceae). African-elodea.

African-elodea is a rooted submerged perennial with alternate leaves. The flowers are from axillary, solitary spathes. The staminate spathes enclose many pedicellate flower buds, whereas the carpellate spathes contain only one sessile flower.

The staminate flower buds are released and rise to the water surface, remaining closed for a short while before eventually opening by the reflexing of perianth parts. The open flower, with three fertile horizontal and three sterile erect stamens, floats on the reflexed perianth. The staminodia function as a sail.

Carpellate flowers are projected to the water surface by an elongate hypanthium (Healy & Edgar, 1980). A meniscus is formed on the water surface by the carpellate flower, which then is slightly below the surface but with the styles protruding above the surface film. As staminate flowers move along the water, propelled by staminodia sails, one flower eventually tips into the meniscus, thereby causing a horizontal fertile stamen to contact an erect stigma.

Lagarosiphon has become an important weed in New Zealand, where it is replacing *Elodea canadensis* that has attained its maximum density and is declining (Healy & Edgar, 1980). Only carpellate plants are known in New Zealand, however, where it spreads by vegetative fragments.

Elodea canadensis Michaux (Hydrocharitaceae). Canadian-pondweed.

Canadian-pondweed is an attached species with cauline leaves in whorls of three. The flowers are axillary, imperfect, and elevated to the water surface by an elongate pedicel on the staminate flower and by an elongate hypanthium on the carpellate flower. The carpellate flower opens by recurving of the sepals and petals, which float on the water surface. The styles spread between the sepals and then recurve, with the tips usually becoming submersed. Upon reaching the surface, the staminate flower opens by the sepals and petals spreading there. The anthers dehisce in an upright position, scattering the pollen onto the surface of the water. Pollen floats on the water surface until it contacts a stigma, initiating germination.

Elodea canadensis is widespread in North America, where it is not known to become weedy. It was introduced into Europe in the early nineteenth century (Cook & Urmi-König, 1985), whereas the first record in Australia is 1931 (Aston, 1973). The European material has almost exclusively been carpellate plants. Vegetative reproduction is mostly from stem fragmentation. Not all nodes, however, are capable of rooting and developing a new plant.

SUBMERSED POLLINATION WITH POLLEN ADHERING TO AIR BUBBLES

Ruppia maritima L. (Potamogetonaceae). Ditch-grass.

Ditch-grass is an annual or perennial of brackish or saline waters with alternate leaves, these having the blades adnate to the stipules for the entire length of the stipules. The flowers are perfect and are produced in a capitate spike that is first enclosed by the sheathing leaf bases. The pollen is four times as long as broad, arcuate, swollen at the ends and at the center on the convex side, and three celled. Its exine is reticulate (Haynes, 1978). The gynoecium is of four or five distinct, stipitate carpels that have the gynophore elongating after anthesis. Pollination is mostly underwater. Following maximum peduncle elongation, the anthers dehisce underwater, releasing pollen that is trapped in air bubbles (Verhoeven, 1979). As the bubbles remain with an inflorescence for several hours, the pollen grains can only contact a stigma of that flower (Verhoeven, 1979), making self-pollination almost certain. Such a system insures ample seed set, which is important for an often annual species.

Out-crossing does occur occasionally in *Ruppia maritima*. Air bubbles, with their trapped pollen grains, break free from the inflorescence occasionally and rise to the water surface. Once on the surface, the bubble breaks, liberating the pollen grains, which float on account of trapped air in the reticulations of the exine. Should they contact a stigma that is at the water surface, cross-pollination occurs. More likely, however, these grains are blown from the *Ruppia* zone.

UNDERWATER POLLINATION

Zannichellia palustris L. (Zannichelliaceae). Horned-pondweed.

Horned-pondweed is an annual rooted plant with alternate, opposite, and occasionally whorled, linear leaves on the same plant. The flowers are imperfect, both staminate and carpellate in the same leaf axil. The carpellate flower is surrounded by a spathelike envelope and consists of four or five separate carpels, each with a funnel-shaped stigma. The staminate flower is outside the envelope, with a filament that projects the anther over the stigmas. Pollen is released in a gelatinous mass (Haynes & Holm-Nielsen, 1987) and falls directly into the funnel-shaped stigma, thus insuring self pollination.

Zannichellia is an annual without any vegetative perennating structure. It therefore depends entirely on seed production for surviving the unfavorable season.

Najas minor All. (Najadaceae). Water nymph.

Najas minor is a rooted, submersed annual with subopposite, serrulate leaves. The plants are monoecious, with flowers solitary in the leaf axils, the staminate flowers mostly above the carpellate ones. Pollination is entirely underwater. The pollen is heavier than water, and, after being released, it slowly descends through the water column, possibly contacting a stigma. Although this is not a system that insures pollination, seed set is very good.

The species occurs in northern Africa, Europe, Asia, and North America (Triest, 1987). In the past 50 years, it has become widespread in eastern North America (Haynes, 1977, 1979; Meriläinen, 1968), where it has become a troublesome weed in some areas. Increase in numbers is mostly from seed. Meriläinen (1968) suggested that the species has been spread by migrating waterfowl.

DISCUSSION

Some species of aquatic vascular plants have become weedy, especially in areas outside their natural ranges. These weedy species have posed environmental problems, either by interfering with recreation, such as by clogging waterways or by lowering the quality of fishing, or by forming breeding areas of noxious insects. Reproduction sufficient to overtake a body of water most often is vegetative, either by stem fragmentation or by production of hibernacula. Almost all species also, at least occasionally, undergo sexual reproduction. Most have very little adaptation for adequate transfer of pollen. Instead, they project the inflorescence above the water for either animal or wind pollination. A few, however, have developed methods of pollen transfer either at the water surface or underwater. Among these few, some, such as *Najas minor*, are annuals and depend entirely on seed production for maintaining the population.

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